STUDIES IN THE AGALINANAE, A SUBTRIBE OF THE RHINANTHACEAE

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THESIS

Presented to the Graduate Faculty of the University of Pennsylvania in Partial Fulfilment of the Requirements for the Degree of Doctor of Philosophy

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THESIS

PRESENTED TO THE FACULTY OF THE GRADUATE SCHOOL OF THE UNIVERSITY OF PENNSYLVANIA, IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Studies in the Agalinanae, a subtribe of the Rhinanthaceae*

FRANCIS W. PENNELL

I. NOMENCLATURE OF THE NEARCTIC GENERA

As here defined the Agalinanae constitute a subtribe of the Buchnereae and include a group of closely allied genera, distinguished from *Buchnera* and its nearer allies only by the normally developed two-celled anthers. These studies concern but a section of this group, all American save for one doubtful record from Madagascar, the genera listed by Von Wettstein in Die Natürlichen Pflanzenfamilien as *Esterhazya* Mikan, *Macranthera* Torr., *Seymeria* Pursh, *Silvia* Benth., and *Gerardia* Linn.

In this paper it is desired to place on a firm basis the nomenclature of the genera occurring in North America north of the Mexican Boundary. This has not proved as easy as anticipated, owing to a misunderstanding of a number of older genera, chief among which is that of *Gerardia* itself.

This paper divides itself naturally into two portions, a history of the genus *Gerardia* (Plumier) Linn., explaining the reason for its rejection as a genus of the Rhinanthaceae, and a history of the Rhinanthaceous genera proposed from time to time under which our species of this group must now be placed. This paper concludes with a summary of the nomenclature it is proposed to follow in these studies.

In 1703 the French traveller and botanist, Charles Plumier, a member of the religious order of the Minimi, published a work, "Nova Plantarum Americanarum Genera," containing descriptions of new genera observed during three voyages to America from 1689 to 1697. One of these is the new genus *Gerardia*.

In this work, a volume of 52 pages of Latin text and 40 plates, I find little mention of the portions of America visited, but in the preface to the same author's "Description des Plantes de L'Amérique" more information is given. He tells us that he went

*Contribution from the Botanical Laboratory of the University of Pennsylvania.

first as aid to M. Surian, charged with a commission from the King of France to the Isles Antilles, "to make search of all that Nature there produces most rare and most curious." During the nearly ten years spent in the West Indies, he described, he says, nearly six hundred different plants.

Gerardia is both described and figured. The description reads:—"Gerardia est plantae genus flore A monopetalo, personato, cujus labium superius surrectum est, subrotundum & emarginatum, inferius vero in tres partes divisum, media bifida. Ex calyce autem C surgit pistillum posticae floris parti B, ad instar clavi infixum, quod deinde abit in fructum D oblongum, gibbum, septo medio E, in duo loculamenta divisum, seminibusque foetum orbicularibus F." Then follows the note,—"Gerardiae unicam speciem vidi. Gerardia humilis, Bugulae foliis, Asphodeli radice."

The genus so founded by Plumier remained unaltered, and very little known, till the first edition of the Species Plantarum in 1753. Here Linnaeus took it up, and to Plumier's species which he named *Gerardia tuberosa*, added four others, *purpurea*, *flava*, *pedicularia* and *glutinosa*. It is evident, being the species adopted by Linnaeus from the original author of the genus, incidentally also being his first species listed, *Gerardia tuberosa* L. must be considered the type of the genus *Gerardia* (Plumier) Linnaeus.*

In addition to the striking feature indicated by the specific name, *tuberosa* is characterized by Linnaeus as "Gerardia foliis subovatis tomentosis repandis, longitudine caulis," points quite at variance from those of his other species with which the name *Gerardia* has come later to be exclusively associated. Yet Linnaeus' list of species, including *tuberosa*, with a few additions from time to time, was copied successively from author to author—by Buc'hoz (1778), Lamarck (1786), J. F. Gmelin (1791), etc., to Willdenow (1800), and Persoon (1807). A few authors of this period realized the incongruity of such treatment, and that logically the name *Gerardia* should apply to *tuberosa* alone.

* Though worked out independently by the writer, this same conclusion was reached a few months earlier by Dr. N. L. Britton. I am indebted to Dr. J. H. Barnhart for reviewing and confirming my determination of the type of *Gerardia*.

First among these was evidently Walter. In his Flora Caroliniana (1788) so far as our North American species are concerned, he relegates *Gerardia* to synonymy, and, not wishing to coin a new name, places *purpurea*, *flava* and *pedicularia* in one of his numerous genera called *Anonymos*.

In 1810 in treating *Gerardia* in Rees' Cyclopedia Sir James E. Smith, after listing first Linnaeus' *tuberosa*, remarks upon its identity being yet doubtful and suggests as a desideratum an examination of its fruit. Then he makes this statement. "Whatever might be the result of such examination this plant must be the true though it were the only *Gerardia*, and the rest in that case must have a new generic appellation and character." This is the first definite assignment of a type species for the genus.

As to the further history of *Gerardia tuberosa* L., after Sir J. E. Smith I find no writer retaining this plant in the Rhinanthaceae. In 1825 Sprengel interpreted it as a synonym of *Ruellia rupestris* Swartz, an Acanthaceous plant, whence in 1847 it was carried into the new genus *Stenandrium* of Nees, becoming a synonym of *Stenandrium rupestre* (Swartz) Nees. If this identification be correct *Stenandrium* Nees should become *Gerardia* (Plumier) L. Though antedating the erection of *Stenandrium* into a genus, such a change was actually made by Rafinesque in his Flora Telluriana in 1838, where *Gerardia tuberosa* L., *G. rupestris* (Swartz) Raf., and *G. scabrosa* (Swartz) Raf. are cited.

In 1835 Bentham in his "Synopsis of the Gerardieae" discusses the past history quite fully, definitely relegates *G. tuberosa* L. to the Acanthaceae, and endorses the earlier selection, practically made by Sprengel, of *G. purpurea* L. as the type. This view has been mostly followed till the present day.

If *Gerardia* is properly an Acanthaceous genus what name is to be applied to our familiar North American species commonly so called?

Of the Linnaean species of this genus to be retained in the Rhinanthaceae three were North American and one Chinese, the latter however not proving a near ally of the others. Species continued to be added from both hemispheres till as late as 1846 when in DeCandolle's Prodromus Bentham finally separated the

series into a number of definitely restricted New World and Old World genera. The Old World genera differ from the New in more points than were realized at that time, so may be definitely dismissed from the present discussion.

After Linnaeus' time the first new names proposed were in 1788 Walter's two genera both named *Anonymos*. These were well characterized; the one might be typified by *Gerardia purpurea* L., the other by a new species *Anonymos cassioides* Walt. Of course the name—or confession of the lack of a name—*Anonymos*, has no value in nomenclature.

In 1791 J. F. Gmelin, reviewing Walter's work, returned his first *Anonymos* to *Gerardia*, but maintained his second *Anonymos* as a new genus *Afzelia*. *Anonymos cassioides* Walt. became *Afzelia cassioides* (Walt.) J. F. Gmel. This genus also was by later authors returned to *Gerardia*, and when in 1814 Pursh became convinced of its generic distinctness, finding the name *Afzelia* meantime applied to a genus of the Caesalpiniaceae, he renamed the genus *Seymeria*. *Afzelia* J. F. Gmel. was restored by Kuntze in 1891. The genus to which this name is applied is a definite, natural group of Mexico and the southern coastal plain region of the United States.

The next generic description in this group is in 1794 that of *Virgularia* described by Ruiz and Pavon from Peru, and based upon their *V. lanceolata*, the specific description of which did not appear till 1798. Though loath with limited material to enter upon any discussion of the South American species of this group, it is necessary to attempt to decide whether this genus can be distinguished from those later proposed to include our North American species.

In the differential characters pointed out by Ruiz and Pavon I find, I confess, little that is convincing. The description of a bifid stigma is surely remarkable, but as no later observer has recorded such a structure in this or in any other South American species of this group, there is doubtless here some error. Also the characters depended upon by Martius (1829) have been shown by Bentham (1835) to be untrustworthy. Since 1835 the name *Virgularia* has been considered a synonym of *Gerardia* L. Yet an inspection of the species of *Virgularia* will, I think, show us

sufficient points of contrast. The material before me is all Bolivian,* but may be safely assigned to this genus.

In *Virgularia* the plant is shrubby, and for our purpose is best distinguished by its tubular, fleshy corolla, mostly red (or some allied shade), after flowering somewhat persistent, shriveling and only tardily falling. These characters appear again, at least in greater part, in the Brazilian *Esterhazya* Mikan, and in our North American *Macranthera* Torr. (to be mentioned later), and seem to indicate a sharp distinction between these three genera and the remainder. *Virgularia* is to be held as a natural, well-marked genus of western South America.

The remainder of this paper will deal strictly with the species of the United States, no other generic name having been proposed from Tropical or South America which can affect the nomenclature of our species. Yet it must be remembered that *a* or *the* great center of this group lies in South America, and no complete understanding of the inter-relationship of the whole can be gained till the species there are studied. Such study is deferred.

The next name that could concern us is in a work descriptive of fruits, *Chytra* Gaertn. fil., 1805. As only the fruit is shown, and that does not seem conclusive—and as no native country whatever is given—this plant may be left permanently as unidentifiable. Such a solution is suggested by Gaertner's specific name *anomala*. Yet it must be recognized that his figure shows a decided resemblance to a "Gerardia" capsule.

In 1819 Rafinesque descrided a yellow-flowered, coarse, lanceolate-leaved plant from Western Kentucky, under a new genus, *Dasistoma*. His description is clear and good, and leaves no doubt that his plant was the one described one year previously (1818) as *Seymeria macrophylla* Nutt. Rafinesque speaks of a short corolla-tube, rotate, 5-lobed limb, 4 nearly equa stamens, short filaments, glabrous anthers, short, cylindrical style, thick, obtuse stigma,—excellent diagnostic characters for *macrophylla*, but all impossible for *Dasistoma* (spelled *Dasystoma*) as taken up in 1846 by Bentham, and followed in later works. *Dasistoma* was based upon *D. aurea* Raf. (1819), antedated by *Seymeria macrophylla* Nutt. (1818), so the combination becomes

**Bang 188, 730, 2530, 2854; Buchtien 129, 789; Rusby 1077, 1078, 1080, 1081.*

D. macrophylla (Nutt.) Raf. (1837). *Seymeria macrophylla* Nutt. was in 1846 made the basis of a section Brachygyne Benth., which in 1903 was raised to a genus *Brachygyne* (Benth.) Small, identical with the older *Dasistoma* Raf. The genus is monotypic.

In 1834 Nuttall described a new genus *Conradia* based upon a large and showy plant, specimens of which he had seen in the herbarium of the Philadelphia Academy of Natural Sciences. His name *Conradia* was antedated by *Conradia* Raf. (1825), and by *Conradia* Mart. (1829), so in 1835, in the account of the plants of Drummond's collection, the name was changed to *Macranthera*. Though this series of articles in the Companion to the Botanical Magazine was mostly the work of the editor, Sir W. J. Hooker, Bentham is to be credited for this genus. In the original description Le Conte's and Bentham's names were both cited after the genus, but in a later article during the same year Bentham tells us *Macranthera* was a manuscript name used by Dr. Torrey in communicating the plant to Dr. Lindley. Doubtless because the collector of the plant in Torrey's herbarium (however described two years later as a second species) Le Conte was mentioned, so with Bentham's explanation Torrey's name may be connected with the plant in question. *Conradia* Nutt. was based upon *C. fuschioides* Nutt., the spelling of which was corrected to *fuchsioides* in the combination *Macranthera fuchsioides* (Nutt.) Benth. However, as this plant had been previously described by William Bartram in his Travels (1791) as *Gerardia flammea*, this species must become **Macranthera flammea** (Bartram) Pennell comb. nov.

In 1835 Bentham reviewed this tribe, adding no new generic names, but systematizing and coördinating the whole, and with another revision in 1846 giving the outline which has been mostly adopted since.

In 1837 Rafinesque undertook the special elaboration of this group in his New Flora of America, adding several new generic names, not giving us a very satisfactory or coördinated treatment, yet showing nevertheless a surprising insight into the group. As I have already had to refer to several of his names, as he proposed a number of genera which must be adopted, and as since his time no new genera have been proposed which he had not already defined, it will be well to go carefully over his treatment.

In the first place, as already recounted, he definitely carried out Sir J. E. Smith's suggestion, and transferred *Gerardia* as a valid genus to the Acanthaceae.

Our Rhinanthaceous species, *Gerardia* of authors and its near allies, he placed in about eight genera, two of which, *Macranthera* "Torr." Benth. and *Seymeria* Pursh, were adopted from other authors, and one, *Dasistoma*, was, as shown above, an earlier genus of his own.

His first genus was *Aureolaria*, created to include the large, perennial, broad-leaved species, and based upon the current interpretation of *Gerardia flava* L. As his *Dasistoma* has been wrongly applied to this group, this first name becomes the correct one for these plants. As *Gerardia flava* L., both by description and the specimen in the Linnaean herbarium, is synonymous with *Rhinanthus virginicus* L., the type-species of the present genus—our pubescent eastern plant—must be known by the name here given it, *Aureolaria villosa* Raf.

His second genus, doubtfully considered distinct from the last, is nearly as uncertain to the present reviewer. *Panctenis* was based upon *Gerardia pedicularia* L. This species and a few close allies agree with *Aureolaria* in broad leaves, yellow flowers, and awned anthers, but their points of disagreement are equally striking. The annual habit of *Panctenis*, its corolla pubescent without, its wingless seeds, constitute several points of difference. I prefer to treat it as a subgenus of *Aureolaria*. The combination *Aureolaria pedicularia* (L.) was made as a variant by Rafinesque.

His third genus, *Agalinis*, in point of numbers is the most important of all. Based upon *Agalinis palustris* Raf., this genus was designed to include all the slender, narrow-leaved, purple-flowered plants, which Bentham later (1846) has treated as his section Eugerardia, and recent writers have come to consider true *Gerardia*. This is a large genus of both North and South America, falling into a number of well-marked subgenera. The type of the genus, *Agalinis palustris* Raf., is the prevalent plant of moist ground, near marshes, from New England to Carolina, Rafinesque correctly interpreting *Gerardia purpurea* L. as intended to include all the purple species. However *G. purpurea* L. is to be typified by the only Linnaean citation with a figure, Plukenet's "Digitalis

virginiana rubra, foliis et facie antirrhini vulgaris," which is unquestionably the current interpretation of the species. *Agalinis palustris* Raf. becomes **Agalinis purpurea** (L.) Pennell comb. nov.

In *Tomanthera* he placed, as *T. lanceolata*, a plant in his herbarium collected in New Jersey by Dr. Cleaver, and cited the species as occurring in Pennsylvania and Carolina. His plant appears to have been undoubtedly *Gerardia auriculata* Michx., described in 1803 from the prairies of Illinois, his specimen being quite small for the species. Possibly the leaves were abnormally entire, or perhaps they were lobed at base and this feature overlooked. His notice of the rarity of the plant is interesting, agreeing with Dr. Darlington and more recent observers of its sporadic occurrence in the East. With *T. lanceolata* he correctly but doubtfully associated *Gerardia auriculata* Michx., though incorrectly as a distinct species. The genus *Tomanthera*, including two species as now understood, is accordingly based upon *T. auriculata* (Michx.) Raf. In 1835 Bentham had based his section Otophylla upon *Gerardia auriculata* Michx., in 1846 raising this to a genus of the same name. *Otophylla* Benth. (1846) therefore becomes a synonym of *Tomanthera* Raf. (1837).

His *Dasistoma* of 1819 was here continued, and, as above shown, *Seymeria macrophylla* Nutt. was identified with it, though as a distinct species. The name *Dasistoma* was here spelled *Dasistema*, and *D. aurea* of 1819 was changed to *D. auriculata*.

Seymeria he adopted unaltered from Pursh.

A genus *Ovostima* was described based upon one species *O. petiolata* from Florida or Alabama. From the description of the plant, the large smooth corolla, bicuspidate anthers, etc., I believe the plant to have been an *Aureolaria*, though the description of the flower as white is surprising. In *Aureolaria* the corolla is fleshy and blackens in drying, not thin and apparently white or very pale ochroleucous as described for *Ovostima*. The plant is left as of doubtful identity.

Macranthera was adopted from Bentham, and for the two species that had then been published, *M. fuchsioides* (Nutt.) Benth. and *M. Lecontei* Torr., he proposed two additional generic names, *Toxopus* and *Tomilix*. As *M. Lecontei* Torr. appears not to have been published till 1837 there is sufficient evidence that

the date on the title page, 1836, is not the date of this volume of Rafinesque's work. *Macranthera fuchsioides* (Nutt.) was yet again described by Rafinesque as *Russelia flammea* based upon Bartram's incidental description of the plant in his Travels as *Gerardia flammea*, and the suggestion made that it is possibly to be considered as a new genus *Flamaria*.

An earlier genus of Rafinesque's, *Pagesia* (1817), reproduced in the New Flora, has been attributed by various authors to *Dasystoma* or *Gerardia*, but certainly does not belong here. Can *Pagesia leucantha* Raf. be identified with *Mecardonia acuminata* (Walt.) Small?

Finally the genus *Dasanthera* Raf., under which in the New Flora he placed *Gerardia cuneifolia* Pursh and *G. fruticosa* Pursh, has no close affinity with this group, nor even harmony within itself. One species, *G. cuneifolia*, had been already identified by Bentham (1835) as *Gratiola acuminata* Walt. (cited as Ell.), so by synonomy would be *Mecardonia acuminata* (Walt.) Small; the other, *G. fruticosa*, by the same author in 1835 was considered a *Pentstemon*, in 1846 as his *P. Lewisii*, a name which Greene (1892) has changed to *P. fruticosus* (Pursh).

Since 1836 there have been but two new generic names proposed for Nearctic species of this group, *Otophylla* Benth. (1846), and *Brachygyne* (Benth.) Small (1903), both of which are antedated by names of Rafinesque's. The present writer has none to add to the sufficient number already published.

A summary of the Nearctic genera of this group, with the type species for each, would be:

AFZELIA J. F. Gmel.; Linn. Syst. Nat. ed. 13. 927. 1791.
—*Anonymos cassioides* Walt.

—*Seymeria* Pursh, Fl. Amer. Sept. 736. 1814.
—*Anonymos cassioides* Walt.

DASISTOMA Raf. Journ. de Phys. **89**: 99. 1819.
—*Dasistoma aurea* Raf. (= *Seymeria macrophylla* Nutt.).

—*Brachygyne* (Benth.) Small, Fl. S. E. U. S. 1073. 1903.
—*Seymeria macrophylla* Nutt.

MACRANTHERA "Torr."; Benth. in Hook. Comp. Bot. Mag. **1**: 174. 1835.

—*Conradia fuchsioides* Nutt. (= *Gerardia flammea* Bartram).

—*Conradia* Nutt. Jour. Acad. Nat. Sci. Phila. **7**: 88. 1834 [not *Conradia* Raf. Neog. 3. 1825; nor *Conradia* Mart. Nov. Gen. et Sp. **3**: 38. 1829].

—*Conradia fuchsioides* Nutt.

—*Flamaria* Raf. New Flor. Amer. **2**: 71. 1837.

—*Gerardia flammea* Bartram.

—*Toxopus* Raf. New Flor. Amer. **2**: 71. 1837.

—*Macranthera Lecontei* Torr.

—*Tomilix* Raf. New Flor. Amer. **2**: 72. 1837.

—*Conradia fuchsioides* Nutt.

AUREOLARIA Raf. New Flor. Amer. **2**: 58. 1837.

—*Aureolaria villosa* Raf.

—*Panctenis* Raf. New Flor. Amer. **2**: 60. 1837.

—*Gerardia pedicularia* L.

(?)—*Ovostima* Raf. New Flor. Amer. **2**: 70. 1837.

—*Ovostima petiolata* Raf.

AGALINIS Raf. New Flor. Amer. **2**: 61. 1837.

—*Agalinis palustris* Raf. (= *Gerardia purpurea* L.).

TOMANTHERA Raf. New Flor. Amer. **2**: 65. 1837.

—*Tomanthera lanceolata* Raf. (= *Gerardia auriculata* Michx.).

—*Otophylla* Benth. in DC. Prodr. **10**: 512. 1846.

—*Gerardia auriculata* Michx.

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* I am indebted to Dr. J. H. Barnhart for the date of this volume.

† No date with paper, cited as 1837 in Index Kewensis.